Infection with behaviour-manipulating parasites enhances bioturbation by key aquatic detritivores

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Abstract

The ecological ubiquity of parasites and their potential impacts on host behaviour have led to the suggestion that parasites can act as ecosystem engineers, structuring their environment and physical habitats. Potential modification of the relationship between parasites and their hosts by climate change has important implications for how hosts interact with both their biotic and abiotic environment. Here, we show that warming and parasitic infection independently increase rates of bioturbation by a key detritivore in aquatic ecosystems (*Gammarus*). These findings have important implications for ecosystem structure and functioning in a warming world, as alterations to rates of bioturbation could significantly modify oxygenation penetration and nutrient cycling in benthic sediments of rivers and lakes. Our results demonstrate a need for future ecosystem management strategies to account for parasitic infection when predicting the impacts of a warming climate.

Introduction

Parasites are found in all ecosystems throughout the globe (Jorge and Poulin, 2018). They comprise up to 40% of all described species (Dobson *et al.*, 2008), feature in up to 70% of the links within food webs (Dunne *et al.*, 2013), and contribute significantly to the biomass of many ecosystems (Kuris *et al.*, 2008). Their presence has important – though still remarkably underappreciated – implications for the structure, functioning and dynamics of entire ecosystems (Amundsen *et al.*, 2009; Dunne *et al.*, 2013). The influence of parasites on how ecosystems respond to environmental change, however, particularly a warming climate (Kutz *et al.*, 2005; Hoberg and Brooks, 2007), remains largely unknown. Climate warming will likely modify rates of parasite transmission (Mouritsen and Jensen, 1997), as temperature is known to influence both parasite infectivity (Studer *et al.*, 2010) and host immunocompetence in invertebrates (Mydlarz *et al.*, 2006). Moreover, by moderating host behaviour (Issartel *et al.*, 2005; Abram *et al.*, 2017), warming influences the susceptibility of organisms to parasites (Morley and Lewis, 2014) and overall host functioning (O'Gorman *et al.*, 2012).

Bioturbation – the mixing of sediment by mobile organisms – is an important ecosystem function that occurs in both terrestrial and aquatic environments. It comprises a key non-trophic mechanism through which organisms physically, chemically, and biologically structure ecosystems (Grant and Daborn, 1994; Jones *et al.*, 1996; Baranov *et al.*, 2016; Wohlgemuth *et al.*, 2017). In aquatic ecosystems, bioturbation influences the flow of nutrients (Mermillod-Blondin *et al.*, 2004), oxygenation of sediments (Baranov *et al.*, 2016), turbidity of the water (Croel and Kneitel, 2011) and sediment erosion rates (Grant and Daborn, 1994). Moreover, the rate of bioturbation has been shown, in a limited number of studies, to increase with warming (Baranov *et al.*, 2016). There is, however, little information about the influence of parasites on rates of bioturbation (Vannatta and Minchella, 2018) and whether this effect is, in turn, modified by warming. Though parasitism has been shown to modify burrowing behaviour in intertidal cockles (Mouritsen and Poulin, 2005), and reduce their digging into the sediments, there have been no studies of which we are aware that found that parasites increase bioturbation rates of their hosts.

Gammarid amphipods contribute significantly to bioturbation in aquatic ecosystems globally (Mermillod-Blondin *et al.*, 2004; Hunting *et al.*, 2012; De Nadaï-Monoury *et al.*, 2013; Vadher *et al.*, 2015), primarily by reworking the uppermost layer (i.e. 2–3 cm) of sediment. In freshwaters, gammarids are also frequently infected with an acanthocephalan parasite, *Polymorphus minutus*, which modifies both the movement of their hosts in the water column and the rates at which they shred detritus (Bauer *et al.*, 2005; Labaude *et al.*, 2016). Two life-stages of the acanthocephalan – the acanthella and the cystacanth – utilize the amphipod intermediate host. The cystacanth is the life-stage associated most strongly with behavioural changes (Bailly *et al.*, 2018), as it is the stage at which the parasite is infective to its definitive (that is, final) host, in this case water fowl.

We explored whether (1) parasitic infection and warming, individually or in combination, modify rates of sediment surface reworking (our measure of bioturbation) by host organisms and, if so, (2) the combined effects of parasitic infection and temperature on host bioturbation

are additive, antagonistic, or synergistic. To address these questions, we quantified the bioturbation activity of *Gammarus duebeni* experimentally in the laboratory across the broad range of temperatures encountered in their native range. *Gammarus* are used frequently as a model system to examine the impacts of parasites on intermediate host behaviour (Bakker *et al.*, 1997; Agatz and Brown, 2014; Perrot-Minnot *et al.*, 2014; Perrot-Minnot *et al.*, 2016) and *G. duebeni* comprise important components of the benthos throughout their native range (Reid, 1938; Donohue *et al.*, 2009; MacNeil and Briffa, 2009), playing a crucial role in ecosystem functioning by processing detritus (Kelly *et al.*, 2002). As the amphipods are ectothermic (Baranov *et al.*, 2016), we expect warming to increase rates of bioturbation by increasing movement capacity (Dell *et al.*, 2011). We also predict that parasitic infection will reduce rates of bioturbation due to reduced interaction between the gammarids and the benthos, as gammarid hosts infected with *P. minutus* display enhanced phototaxis and are more likely to move upward in the water column (Perrot-Minnot *et al.*, 2016). As temperature and parasitic infection have been shown to additively impact similar gammarid behaviours (Labaude *et al.*, 2016), we expect warming and parasites to additively impact bioturbation.

Methods

Experimental design

We quantified the rate of sediment surface re-working by adult *Gammarus duebeni* var. *celticus* at two levels of infection (*i.e* infected or uninfected by *P. minutus* cystacanths) and at four temperatures (4 °C, 9 °C, 14 °C, and 19 °C), encompassing the majority of the temperature range experienced by *G. duebeni* in their native range in Ireland, in a full-factorial experiment. Each experimental treatment combination was replicated 20 times.

Amphipods, benthic lake sediments and lake water used in the experiment were collected from Lough Lene, Co. Westmeath, Ireland (53.6625°N, 7.2340°W) on 22 January 2018. Surficial (i.e. less than 3 cm depth) benthic lake sediments were collected, homogenized, passed through a 1 mm sieve to remove macrofauna and rocks, and allowed to settle in lake water for one day before use.

Bioturbation was quantified based upon methods developed by De Nadaï-Monoury *et al.* (2013) and Wohlgemuth *et al.* (2017). Eight 10 L buckets (28.5 cm diameter, 20 cm in height) were filled with lake sediments to a depth of 5 cm. Sterile centrifuge tubes (8.5 cm long with an internal diameter of 2.7 cm) with their tops and bottoms removed were placed into the buckets (25 pipes per bucket). Tracer sand (pink luminophores <125 μm; Brianclegg Ltd., UK) was then added to a depth of 0.2 cm within each tube. Filtered aerated lake water was then added slowly to the bucket to a depth of 13 cm above the sediment. A single *G. duebeni* adult (>0.02 g fresh weight) was added to individual tubes, which were then covered with mesh (1 mm aperture) to retain the organisms within the tubes whilst allowing the circulation of aerated water. Presence of the mesh also enabled clinging behaviour by *Gammarus*, thus allowing them to mimic their propensity to cling to floating debris in the water column. Each 10 L bucket contained ten tubes containing infected *G. duebeni*, ten tubes with uninfected *G. duebeni*, and five tubes containing no *G. duebeni*. The latter acted as procedural controls. Fresh mass of *G. duebeni* individuals at the commencement of the experiment was similar across all experimental treatment combinations (ANOVA; $F_{7,135} = 1.7$, $P = 0.12$). Sediment disturbance in the procedural controls was negligible (Fig. S1), and did not vary with temperature (ANOVA, $F_{3,36} = 0.73$, $P = 0.54$). Two 10 L buckets were kept at each of the four temperatures analysed. The buckets

were aerated continually and kept in a 12 h:12 h light:dark cycle. After 28 days, *G. duebeni* individuals were removed and dissected to ensure infection status. Only organisms with single, cystacanth-stage infections were designated as infected – any hosts with multiple-infections or acanthellae-stage infections were omitted from analyses. Parasites were then examined microscopically to confirm their identity morphologically (following McDonald, 1988) after cystacanths were first placed in a 0.25 m$_M$ solution of sodium taurocholate, a type of bile salt which encourages extension of the proboscis, and left overnight at 37 °C.

Data analyses

Photographs of the sediment surface of each experimental tube were taken with a Canon EOS 550D (Aperature: f/4.5; Pixels: 5184 × 3456) and saved as RGB-coloured JPEGs. Images were captured under UV light (395 nm wavelength, UV LED flashlight, LightingEVER, Las Vegas, USA) to optimise fluorophore detection. Images were then processed using ImageJ (version 1.43u; US National Institutes of Health, https://imagej.nih.gov/ij/). Images were cropped, then split into red, green and blue colour channels. The red channel was selected for analyses, as it allowed for clearest distinction between the pink fluorophores and the black lake sediments. Images were then thresholded in order to colour the fluorescent particles white and the sediment particles black. The photo was then analysed and the proportion of black pixels, representing the lake sediments brought up from below the fluorophores, recorded. The total area of surface sediment reworked was then quantified in cm^2.

Data were analysed in R (version 3.4.1; R Core Team, 2017). The extent of sediment surface reworking was log$_{10}$-transformed prior to analyses to meet assumptions of normality and homoscedasticity. A linear mixed-effects model was constructed using lme4::lmer (Bates *et al.*, 2015), with the log$_{10}$-transformed area reworked as the response variable, bucket as a random effect, and temperature and infection status as fixed effects. Model selection was done with model.sel:MuMIn (Barton, 2016). We report the results of fixed effects on the model with the lowest AIC of the candidate models. To determine the magnitude of the effect of infection across the range of temperatures examined, we calculated the Cohen's *d* effect size with 95% confidence intervals using effsize:cohen.*d* (Torchiano, 2018).

Results

Infected individuals of *G. duebeni* reworked significantly more sediment surface area than uninfected individuals (linear mixed-effects model, $F_{1,137} = 7.38$, $P < 0.01$; Fig. 1A). Rates of sediment reworking also increased significantly with warming ($F_{8,137} = 5.3$, $P = 0.05$; Fig. 1A). Combined effects of parasitic infection and warming were, however, additive, as temperature did not interact with parasitic infection in moderating bioturbation, and the magnitude of the effect of parasitism was consistent across the range of temperatures examined (Fig. 1B).

Discussion

We found that both parasitic infection and warming increased bioturbation by *G. duebeni* in our experimental microcosms. Moreover, infection and temperature moderated bioturbation additively and did not interact. This comprises the first evidence of which we are aware of parasites enhancing the bioturbation activity of their hosts. Given the importance of gammarid amphipods as key drivers of detritivory and bioturbation in freshwater ecosystems (Hunting *et al.*, 2012), coupled with predicted increases in the prevalence of parasites in a warmer world
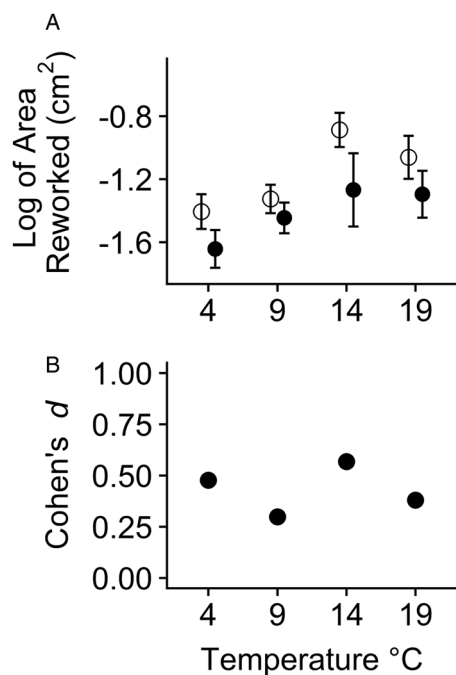
Fig. 1. (A) Rates (mean ± s.e.) of bioturbation by *G. duebeni* infected (open circles) and uninfected (closed circles) with *P. minutus* across a temperature range of 4 °C to 19 °C. Bioturbation was measured as the area of benthic surface sediments in our experimental microcosms that were reworked over the course of the experiment. (B) Effect size of *P. minutus* infection on bioturbation rates by *G. duebeni* across the range of temperatures examined.

(Galaktionov, 2017), our findings have important implications for the structure and functioning of freshwater ecosystems under global change.

The observed enhanced bioturbation caused by infection with *P. minutus* contrasts with our *a priori* predictions. As infection with *P. minutus* increases movement upwards in the water column (Jacquin *et al.*, 2014; Perrot-Minnot *et al.*, 2016; Bailly *et al.*, 2018), we anticipated that infected hosts would interact less with the benthos, leading to a decrease in the rates of surface sediment reworking. However, parasites often do not have fine-scale control when manipulating their hosts. The manipulation of crickets by nematomorph worms provides a clear example. The worms alter the behaviour of crickets to increase their chances of entering the water. However, the manipulation is not a specific push towards the water, but rather results in an increase in erratic jumping (Thomas *et al.*, 2002). It has been suggested previously that the behavioural manipulation of our model parasite, *P. minutus,* is non-specific and does not drive the intermediate host directly to the exact, preferred definitive host (Jacquin *et al.*, 2014). The mechanism of manipulation by the parasite is possibly related to hypoxia in the water column and anaerobic metabolism within the host (Perrot-Minnot *et al.*, 2016). The mechanisms underlying the manipulation are not yet understood, though it is possible that an accumulation of lactate in the brain of the amphipods may drive the reversal in geotaxis seen with *P. minutus* infection (Perrot-Minnot *et al.*, 2016). The increased digging we observed in infected *G. duebeni* may therefore reflect an additional impact of lactate accumulation in the brain and a consequential increase in movement, rather than a mechanism for directly increasing transmission of the parasite to its definitive host. However, further work is needed to determine whether or not enhanced bioturbation activity is adaptive for the parasite.

A wide range of animal behaviours exhibit thermal dependence, many of which can be explained by metabolic theory

(Kordas *et al.*, 2011; Dell *et al.*, 2014). Higher temperatures have been linked previously to enhanced bioturbation rates in non-amphipod aquatic species (Ouellette *et al.*, 2004), though the extent to which temperature enhances or supresses bioturbation likely varies across species (Maire *et al.*, 2010). Our results are consistent with those from previous studies (Labaude *et al.*, 2016) that found additive, rather than interactive, effects of temperature and parasitic infection on a range of behaviours in *Gammarus*. As the climate continues to warm, alterations in the prevalence of parasites and associated shifts in the behaviour and functioning *of Gammarus* have the potential to moderate the impact of many of the stressors of aquatic systems associated with global environmental change (Baranov *et al.*, 2016).

Our results demonstrate a significant influence of parasites on the key ecosystem function that is bioturbation (Vannatta and Minchella, 2018). Bioturbation has, for example, been linked to rates of community respiration, sediment transport, nutrient availability and overall community structure (Grant and Daborn, 1994; Ouellette *et al.*, 2004; Donohue and Garcia Molinos, 2009; Croel and Kneitel, 2011; Baranov *et al.*, 2016; Wohlgemuth *et al.*, 2017). Therefore, irrespective of whether or not the altered behaviour we found is adaptive in terms of the parasite's fitness, our findings have important implications for our understanding of the roles played by parasites in the structure and functioning of aquatic systems.

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